Bull. Mus. natn. Hist. nat., Paris, 4e sér., **9**, 1987,
section B, *Adansonia* nº 2 : 167-175.

Species vicariance in the Mexican flora and description of a new species of *Salvia* (*Lamiaceae*)

T. P. Ramamoorthy & D. H. Lorence

Summary : The previously overlooked role of vicariance in contributing to species richness in the Mexican flora is discussed. Examples of vicariant species pairs in four genera belonging to three families are presented : *Ruellia* (*Acanthaceae*), *Salvia* (*Lamiaceae*), *Deppea* and *Randia* (*Rubiaceae*). Evolution of these and other vicariants probably occurred through fragmentation of ancestral populations and subsequent differentiation by allopatry. A new species of *Salvia* (*S. manantlanensis* Ramamoorthy) is described.

Résumé : Le rôle de la vicariance, auparavant négligé, et sa contribution à l'enrichissement de la flore mexicaine sont discutés. Des exemples d'espèces vicariantes de quatre genres appartenant à trois familles sont présentés : *Ruellia* (*Acanthaceae*), *Salvia* (*Lamiaceae*), *Deppea* et *Randia* (*Rubiaceae*). Leur évolution, ainsi que celle d'autres vicariants, s'est probablement produite de manière allopatrique par fragmentation des populations ancestrales suivie de différenciation. Une nouvelle espèce de *Salvia* (*S. manantlanensis* Ramamoorthy) est décrite.

T. P. Ramamoorthy, Instituto de Biologia, Apartado Postal 70-233, Universidad Nacional Autónoma de México, Del. Coyoacán, C.U., 04510 México, D.F., México.
David H. Lorence, Pacific Tropical Botanical Gardens, P.O. Box 340, Kawai, Hawaii, 96765, U.S.A.

The flora of Mexico is not only rich, with over 20,000 species of vascular plants (Rzedowski, 1978), but is also of great phytogeographical interest as its elements are made up of three different floristic provinces : the Madrean, the Caribbean and Californian (Takhtajan, 1969 ; Raven & Axelrod, 1978). In addition, both generic and specific endemism appear to be quite high. Among the vascular plants we estimate species endemism to be as high as 60-65 % and the number of genera endemic to Mexico to exceed 300 (Ramamoorthy & Lorence, submitted).

Among the factors that contribute to species richness in Mexico, vicariance appears to be a primary one, although it seems to have been previously overlooked judging by its absence from literature on Mexican botany (e.g., Kaplan Langman, 1964). Cain (1944) defined vicarious species as "closely related allopatric species which have descended from a common ancestral population and attained spatial isolation". Cutler (1972) demonstrated vicariance in intercontinental groups, and Bramwell (1972) documented it in the flora of Canary Islands. Vicarious species in the montane floras of Europe and East Africa have been discussed by Kornas (1972) and Hedberg (1972). In our studies we have come across a number of examples of vicariance in the Mexican flora and present four of these here.

RUELLIA L.

Ruellia L. (*Acanthaceae*) of the tribe *Ruellieae* Nees *emend.* Bremekamp (1944) is a large, morphologically variable genus of 250 species or more and is both tropical and subtropical in distribution. The morphological variation displayed by the species of this genus is impressive, and their taxonomy is involved. LINDAU's (1895) circumscription is adopted here, and the unifying characters are the contorted aestivation of the corolla lobes and the spheroidal or ellipsoidal, three or more porate, reticulate, spinulose or banded pollen grains.

The primary centers of diversity of the genus are Indo-Malaya, Brazil, Africa, and Mexico and Central America (LONG, 1970). In Mexico the genus is represented by over 40 species, and the occurrence of many of these species is very local, suggesting evolution by fragmentation. The variation in the shape, size and color of the corolla is very pronounced, and this may be due to adaptation to various pollinators. Among the several species pairs in the genus occurring in Mexico, *Ruellia bourgaei* Hemsl. and *R. palmeri* Greenm. constitute an excellent example.

Both species are characterized by their large, gibbous corollas with exserted stamens, and both are apparently visited by bats (CHAVEZ, 1974; W. LOPEZ-FORMENT, pers. comm.). The pale green, pale yellow or white corollas are strikingly similar in shape, differing only in their sizes (Fig. 1, *a, d*). The two are further distinguished from one another by their petioles : winged in *R. bourgaei* (Fig. 1, *b*), unwinged in *R. palmeri* (Fig. 1, *c*), and by their inflorescences : an elongate raceme in the former (Fig. 1, *c*), and a condensed raceme in the latter (Fig. 1, *f*). In addition, the two species are geographically isolated (Fig. 3). *Ruellia bourgaei* is presently known from the states of Jalisco through Hidalgo, the Distrito Federal to Puebla where it is generally found above 1,600 m, whereas *R. palmeri* occurs from Michoacan through Guerrero to Oaxaca and is generally found below 1,600 m. The remarkable similarities in floral structure suggest a commong origin for these two species, but their differentiation is largely due to allopatry, probably reinforced by selection by bats.

SALVIA L.

Salvia L. (*Lamiaceae*) of the tribe *Monardeae* (BENTHAM, 1848) is a large genus of about 900 species (STANDLEY & WILLIAMS, 1973) distributed in both tropical and subtropical parts of the world. In the Americas the genus is represented by over 500 species (STANDLEY & WILLIAMS, 1973), most of which belong to *Salvia* subg. *Calosphace* (EPLING, 1936, 1939). In Mexico, *Salvia* is represented by over 275 species (RAMAMOORTHY, 1984*a*, 1984*b*, 1984*c*). These species of *Salvia* subg. *Calosphace* have been placed in 105 sections (EPLING, 1936, 1939, 1957), many of which are difficult to tell apart, suggesting monophyly for the group. The variation in Mexican *Salvia* is very pronounced, and the genus occurs predominantly in the *Pinus, Quercus,* and *Abies* forests, usually above 1,000 m. There are a number of examples of species pairs in the genus in Mexico, and one is presented here.

Two blue flowered species belonging to *Salvia* sect. *Uliginosae* are closely related and allopatric : *S. hintonii* Epling from Guerrero and *S. manantlanensis* Ramamoorthy from

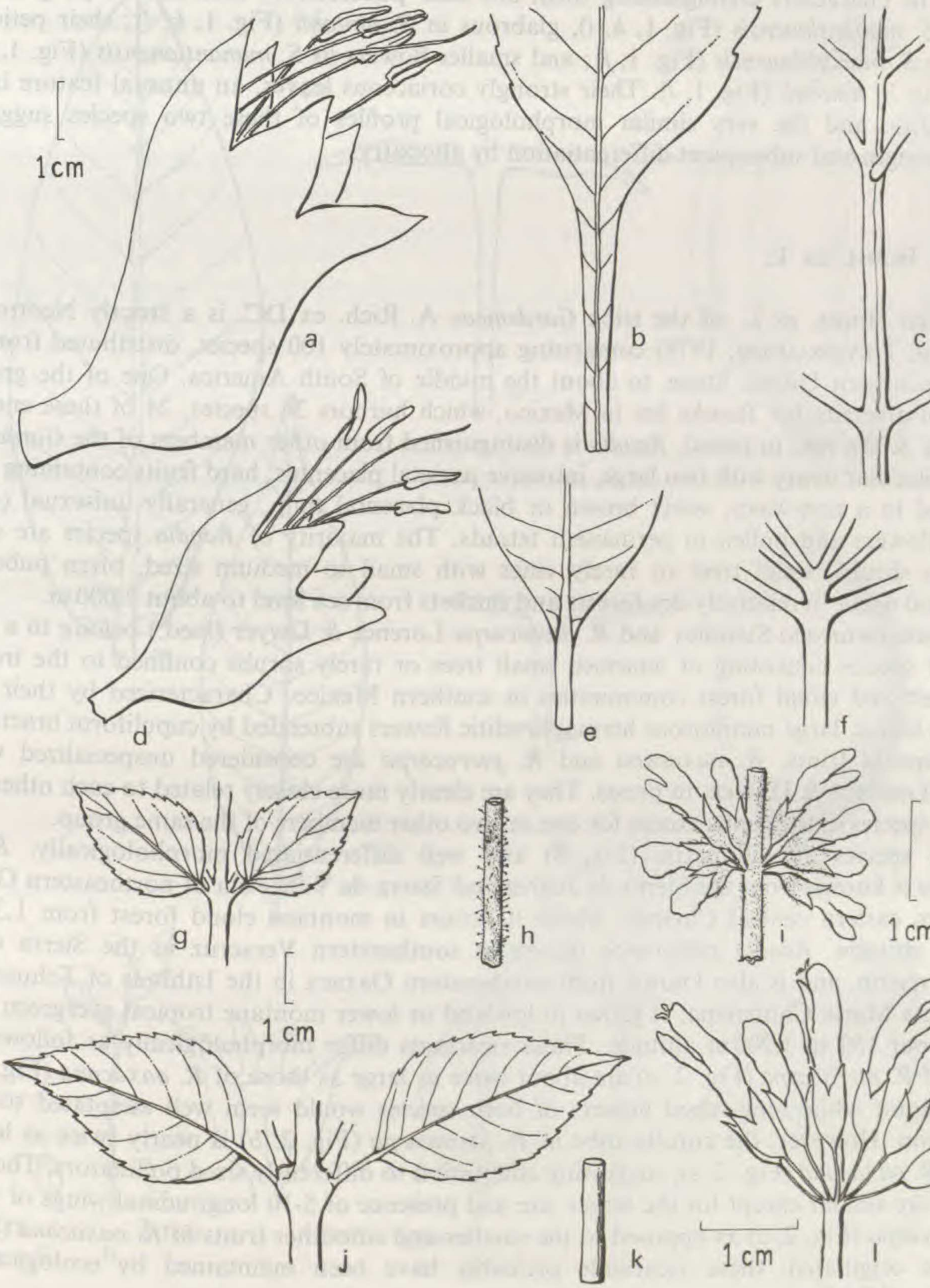

FIG. 1. — **Ruellia bourgaei** : **a**, flower ; **b**, petiole ; **c**, axis of inflorescence (all *Pringle 4500*, MEXU). — **Ruellia palmeri** : **d**, flower ; **e**, petiole ; **f**, axis of inflorescence (all *Ernst 2560*, MEXU). — **Salvia manantlanensis** : **g**, node with leaves ; **h**, stem ; **i**, verticil of flowers (all *Sorensen et al. 7968*, MEXU). — **Salvia hintonii** : **j**, node with leaves ; **k**, stem ; **l**, verticil of flowers (all *Hinton 14096*, MEXU).

Jalisco. The characters distinguishing them are their pubescence : stem and calyx glandular hairy in *S. manantlanensis* (Fig. 1, *h, i*), glabrous in *S. hintonii* (Fig. 1, *k, l*); their petioles : shorter in *S. manantlanensis* (Fig. 1, *j*); and smaller flowers in *S. manantlanensis* (Fig. 1, *i*) as opposed to *S. hintonii* (Fig. 1, *l*). Their strongly coriaceous leaves, an unusual feature in the genus *Salvia*, and the very similar morphological profiles of these two species suggest a common origin and subsequent differentiation by allopatry.

RANDIA Houst. ex L.

Randia Houst. ex L. of the tribe *Gardenieae* A. Rich. ex DC. is a strictly Neotropical genus (e.g. TIRVENGADUM, 1978) comprising approximately 100 species, distributed from the extreme southern United States to about the middle of South America. One of the greatest centers of diversity for *Randia* lies in Mexico, which harbors 34 species, 24 of these endemic (LORENCE & DWYER, in press). *Randia* is distinguished from other members of the *Gardenieae* by its unilocular ovary with two large, intrusive parietal placentas, hard fruits containing seeds embedded in a non-waxy, sweet brown or black placental pulp, generally unisexual (4-) 5-merous flowers and pollen in permanent tetrads. The majority of *Randia* species are spiny, dioecious shrubs, small trees or rarely vines with small to medium sized, often pubescent leaves, and occur in relatively dry forests and thickets from sea level to about 2,000 m.

Randia oaxacana Standley and *R. pterocarpa* Lorence & Dwyer (ined.) belong to a small group of species consisting of unarmed small trees or rarely shrubs confined to the tropical rain forest and cloud forest communities in southern Mexico. Characterized by their large glabrous leaves, large ramiflorous hermaphroditic flowers subtended by cupuliform bracts, and large ellipsoid fruits, *R. oaxacana* and *R. pterocarpa* are considered unspecialized within *Randia* (LORENCE & DWYER, in press). They are clearly more closely related to each other than to other species in the genus except for one or two other members of the same group.

The species are allopatric (Fig. 3) and well differentiated morphologically. *Randia oaxacana* is known from the Sierra de Juárez and Sierra de Villa Alta of northeastern Oaxaca and from eastern central Chiapas, where it occurs in montane cloud forest from 1,300 to 2,300 m altitude. *Randia pterocarpa* occurs in southeastern Veracruz in the Sierra de los Tuxtlas region, and is also known from southeastern Oaxaca in the Isthmus of Tehuantepec near Santa María Chimalapa. It grows in lowland or lower montane tropical evergreen forest from about 150 to 1,200 m altitude. These vicariants differ morphologically as follows. The leaves of *R. pterocarpa* (Fig. 2, *a*) are about twice as large as those of *R. oaxacana* (Fig. 2, *d*). The fragrant white long-tubed flowers of both species would seem well adaptated to moth pollination. However, the corolla tube in *R. pterocarpa* (Fig. 2, *b*) is nearly twice as long as that of *R. oaxacana* (Fig. 2, *e*), suggesting adaptation to differently sized pollinators. The fruits of both are similar except for the larger size and presence of 5-10 longitudinal wings or ribs in *R. pterocarpa* (Fig. 2, *c*) as opposed to the smaller and smoother fruits of *R. oaxacana* (Fig. 2, *f*). Once originated, these vicariants probably have been maintained by ecological and pollinator differences.

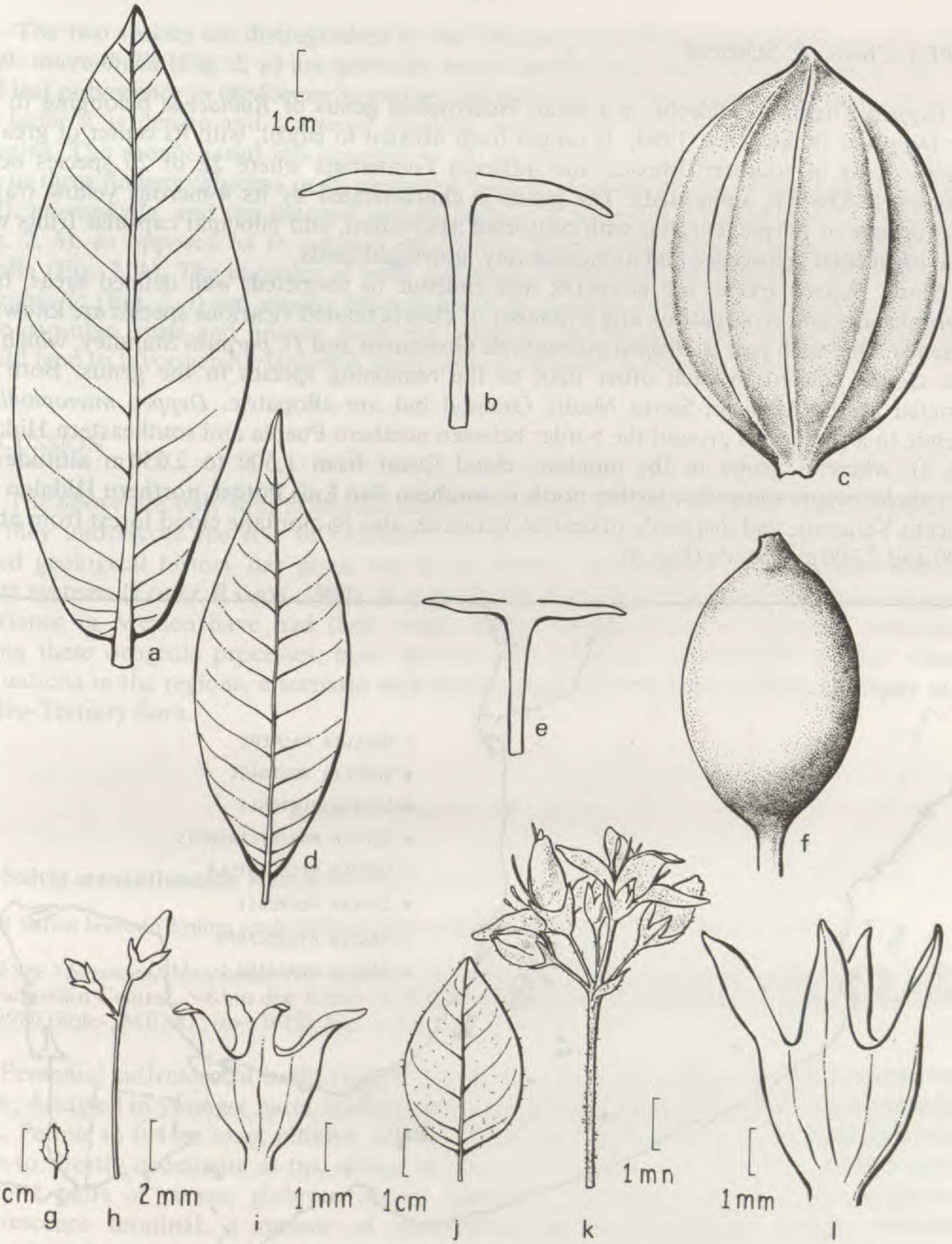

FIG. 2. — **Randia pterocarpa** : **a**, leaf ; **b**, corolla (both *Dressler & Jones 29*, MEXU) ; **c**, fruit (*Calzada 811*, MEXU). — **Randia oaxacana** : **d**, leaf ; **e**, corolla (both *Lorence 4189*, MEXU) ; **f**, fruit (*Lorence 4374*, MEXU). — **Deppea microphylla** : **g**, leaf ; **h**, inflorescence ; **i**, fruit (all *Hernandez 4186*, MEXU). — **Deppea purpusii** : **j**, leaf ; **k**, inflorescence ; **l**, fruit (all *Medillin s.n.*, April 1910, MEXU).

DEPPEA Chem. & Schlecht.

Deppea Chem. & Schlecht. is a small Neotropical genus of *Rubiaceae* belonging to the tribe *Deppeeae* (KIRKBRIDE, 1984). It ranges from Mexico to Brazil, with its center of greatest diversity lying in southern Mexico and adjacent Guatemala where 22 of 25 species occur (LORENCE & DWYER, submitted). The genus is characterized by its 4-merous yellow (rarely white, orange or purple) corollas with contorted aestivation, and bilocular capsular fruits with apical loculicidal dehiscence and numerous tiny, unwinged seeds.

Many *Deppea* species are allopatric and endemic to restricted, well defined areas, both geographically and ecologically, and a number of closely related vicarious species are known in the genus. One such pair is *Deppea microphylla* Greenman and *D. purpusii* Standley, which are more closely related to each other than to the remaining species in the genus. Both are restricted to the Mexican Sierra Madre Oriental but are allopatric. *Deppea microphylla* is endemic to a small area around the border between northern Puebla and southeastern Hidalgo (Fig. 3), where it grows in the montane cloud forest from 1,500 to 2,050 m altitude. *D. microphylla* occurs somewhat farther north in southern San Luis Potosi, northern Hidalgo and adjacent Veracruz, and disjunctly in central Veracruz, also in montane cloud forest from about 1,000 and 2,200 m altitude (Fig. 3).

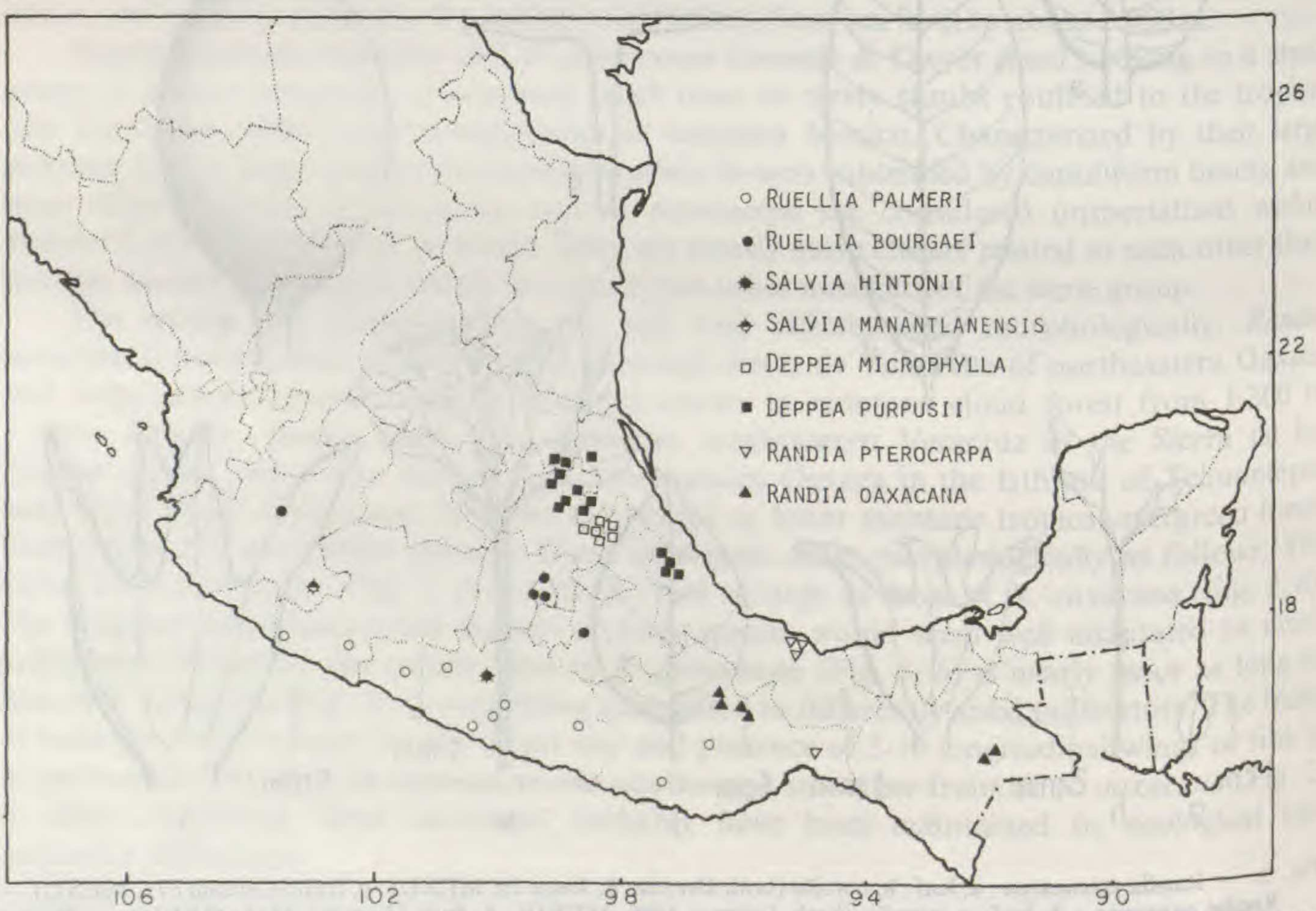

FIG. 3. — Southern Mexico, showing distribution of *Ruellia bourgaei, R. palmeri, Salvia manantlanensis, S. hintonii, Deppea microphylla, D. purpusii, Randia oaxacana* and *R. pterocarpa*.

The two species are distinguished by the following morphological differences. The leaves of *D. microphylla* (Fig. 2, *g*) are generally much smaller than those of *D. purpusii* (Fig. 2, *j*), and leaf pubescence in the former is sparser and restricted to the margins and veins, whereas in the latter it is denser and scattered over the adaxial leaf surface as well as the veins and margins. The monochasial inflorescence in *D. microphylla* is reduced and composed of only one to three flowers, whereas in *D. purpusii* it is (2-)4-14-flowered. The flowers are also smaller in *D. microphylla*, and the external corolla surface is glabrous or rarely with scattered hairs (Fig. 2, *h*), as opposed to *D. purpusii* which has larger flowers with a moderately hirtellous corolla (Fig. 2, *k*). The capsules of both species are similar morphologically, but those of *D. microphylla* (Fig. 2, *i*) are smaller than those of *D. purpusii* (Fig. 2, *l*). All species of *Deppea* have capsular fruits and minute seeds not adapted for dispersal over long distances, which would tend to favor genetic isolation and resulting vicarism in fragmented populations.

DISCUSSION

The above are only four examples selected from among many possible ones; however, we feel they underscore the role of vicariance in the evolution of the Mexican flora. Mexico's varied geological history has given rise to its present day complex of mountain, river and desert systems (LOPEZ RAMOS, 1982). It is probable, then, that numerous incidence of species vicariance in Mexico have had their origin in the fragmentation of ancestral populations during these orogenic processes, both tectonic and volcanic, accompanied by past climatic fluctuations in the regions, a scenario well documented by AXELROD (1958) in his study of the Madro-Tertiary flora.

A NEW SPECIES OF *SALVIA* L.

Salvia manantlanensis Ramamoorthy, *sp. nov.*

A Salvia hintonii Epling *caule trichomatibus glanduliferis et petiolo breviore distinguinda.*

TYPE : *Sorensen, Matekaitis, Iltis & Shatz 7968*, Mexico : Jalisco, El Chante, upper E slope of Sierra de Manantlán Central, 5-6 km due South of Rincón de Manantlán, *Pinus-Quercus* forest, 2,200-2,400 m, 12.1.1980 (holo-, MEXU ; iso-, WIS). Fig. 1, *g-i*.

Perennial suffrutescent herbs (height not known) with thick rhizome. Stem mostly terete below, 4-angled in younger parts, tomentose to villous with white multicelled, viscid, glandular hairs. Petiole to 0.4 cm long, pinkish, white villous; leaf-blades ovate, rarely ovate-lanceolate, acute to shortly acuminate at tip, obtuse at base, 2-5 cm long, 1-2.5 cm wide, crenate-serrate, with 4-5 pairs of nerves, glabrous above, markedly glandular-punctate below, coriaceous. Inflorescence terminal, a raceme of interrupted, up to 12-flowered whorls; internodes separating whorls 0.4-4 cm long, tomentose with spreading viscid glandular hairs. Bracts ovate, acuminate, ca. 0.7 cm long, ca. 0.5 cm wide, drying dark red, pilose with white hairs, early deciduous. Pedicel to 0.6 cm long, tomentose with viscid glandular hairs. Calyx ca. 0.7 cm long, ca. 0.3 cm wide, maroon, densely tomentose with viscid glandular hairs, bearing scattered

sessile glands between nerves, 3-lobed, upper one 7-nerved, all lobes long acuminate. Corolla 1.6 cm long (tube ca. 0.8 × 0.3 cm, glabrous, epapillate), lilac, blue or white, the upper lip ca. 0.6 cm long, galeate, densely bearded, bearing scattered sessile glands, the lower lip ca. 0.8 cm long, bearing many sessile glands below towards the base, 3-lobed, the laterals shorter, rounded, the middle larger, ca. 0.4 × 0.6 cm, undulate, indistinctly bilobed. Stamens 2, included, filament ca. 2.2 mm long, the rudder ca. 4 mm long, 1 mm wide, produced into an acuminate tooth above, the connective ca. 3 mm long, the anther ca. 1.2 mm long, the connective at point of articulation with the filament produced into a downward facing globose tooth. Ovules to 1 mm tall; gynobase horn as tall as the ovules; style 1.3 cm long, densely bearded above, divided with the upper fork longer than the lower. Seeds presently not known. Flowering January.

MATERIAL STUDIED. — MEXICO : Jalisco, El Chante, Upper E slope of Sierra de Manantlán Central, on lumber road S of San Miguel "meadows", 5-6 km due S of Rincón de Manantlán, *Iltis et al. 2609* (MEXU, WIS), *Sorensen et al. 7968* (type); ca. 6 km WSW of Rincón de Manantlán, *Iltis et al. 1323* (MEXU, WIS).

ACKNOWLEDGMENT : We thank Elvia ESPARZA for Figures 1 and 2, Felipe VILLEGAS for Figure 3, and Fernando CHIANG for the Latin diagnosis; CONACYT (Mexico) grants PCCBBNA 021142 to TPR and PCECBNA 021719 to DHL are gratefully, acknowledged.

REFERENCES

AXELROD, D. I., 1958. — Evolution of the Madro-Tertiary Geoflora. *Bot. Rev.* 24 : 433-509.

BENTHAM, G., 1848. — Labiatae. *In* CANDOLLE, A. P. DE, *Prodromus* 12 : 27-603.

BRAMWELL, D., 1972. — *Endemism in the flora of the Canary Islands. In* VALENTINE, D. H., *Taxonomy, Phytogeography and Evolution*. Academic Press, London, New York : 141-159.

BREMEKAMP, C. E. B., 1944. — Materials for a monograph of the Strobilanthinae (Acanthaceae). *Verh. Nederl. Akad. Wet. Afd. Natuurk.*, sect. 2, 41 (1) : 1-306, pl. 1-6.

CAIN, S. A., 1944. — *Foundations of Plant Geography*. Harper, New York.

CHAVEZ, P. R., 1974. — Observaciones en el polen de plantas con probable polinización quiropterófila. *An. Esc. Nac. Cienc. Biol., Méx.* 21 : 115-143.

CUTLER, D. F., 1972. — *Vicarious species of Restionaceae in Africa, Australia and South America. In* VALENTINE, D. H., *Taxonomy, Phytogeography and Evolution*. Academic Press, London, New York : 73-83.

EPLING, C., 1936. — Synopsis of the South American Labiatae. *Repert. Spec. Nov. Regni Veg. Beih.* 85 (1-3) : 1-288.

EPLING, C., 1939. — A revision of Salvia subgenus Calosphace. *Repert. Spec. Nov. Regni Veg. Beih.* 110 : 1-383.

EPLING, C., 1957. — Supplementary notes on American Labiatae. *Brittonia* 8 : 297-313.

HEDBERG, O., 1973. — *Adaptive evolution in a tropical-alpine environment. In* HEYWOOD, V. H., *Taxonomy and Ecology*. Academic Press, New York, London : 71-92.

KAPLAN LANGMAN, I., 1964. — *A Selected Guide to the Literature on the Flowering Plants of Mexico*. University of Pennsylvania Press, 1015 p.

KIRKBRIDE, J. H., Jr., 1984. — Manipulus Rubiacearum III. Deppeeae, a new tribe of Rubioideae (Rubiaceae). *Brittonia* 36 (3) : 317-320.

KORNAS, J., 1972. — *Corresponding taxa and their ecological background in the forests of temperate Eurasia and North America. In* VALENTINE, D. H., *Taxonomy, Phytogeography and Evolution.* Academic Press, London, New York : 37-59.

LINDAU, G., 1895. — Acanthaceae. *Nat. Pflanzenfam.* IV, 36 : 274-354.

LONG, R. W., 1970. — The genera of Acanthaceae in the Southeastern United States. *J. Arnold Arb.* 51 (3) : 257-309.

LOPEZ RAMOS, E., 1982. — *Geologia de México.* Vol. 1-3. Edicion Escolar, México, D.F.

LORENCE, D. H. & DWYER, J. D., (in press). — New taxa and a name in Mexican and Central American *Randia* (Rubiaceae, Gardenieae). *Bol. Soc. Bot. México* 47.

LORENCE, D. H. & DWYER, J. D., (submitted). — A revision of *Deppea* (Rubiaceae). (Submitted to *Ann. Missouri Bot. Gard.*).

RAMAMOORTHY, T. P., 1984*a*. — Notes on *Salvia* (Labiatae) in Mexico with three new species. *J. Arnold Arb.* 65 : 135-143.

RAMAMOORTHY, T. P., 1984*b*. — A new species of *Salvia* (Lamiaceae) from the Sierra de Los Tuxtlas. *Pl. Syst. Evol.* 146 : 141-143.

RAMAMOORTHY, T. P., 1984*c*. — A new species of *Salvia* (Lamiaceae) from Mexico. *Brittonia* 36 : 297-299.

RAMAMOORTHY, T. P. & LORENCE, D. H., (submitted). — Generic endemism in the Mexican flora. (Submitted to *J. Arnold Arb.*).

RAVEN, P. H. & AXELROD, D. I., 1978. — Origin and relationships of the California flora. *Univ. Calif. Publ. Bot.* 72 : 1-134.

RZEDOWSKI, J., 1978. — *Vegetación de México.* Limusa, Mexico, D.F.

STANDLEY, P. C. & WILLIAMS, L. O., 1973. — Labiatae, in Flora of Guatemala. *Fieldiana, Bot.*, 24 (9) : 237-317.

TAKHTAJAN, A., 1969. — *Flowering plants : Origin and Dispersal.* Smithsonian Institution Press, Washington, D.C.

TIRVENGADUM, D. D., 1978. — A synopsis of the Rubiaceae-Gardenieae of Ceylon (Sri Lanka). *Bull. Mus. Nat. Hist. Nat.* (*Paris*), 3e sér., nº 521, Nov.-Déc. 1978, Botanique, 35 : 3-33.